SELECTION OF NEST AND ROOST TREES BY PILEATED WOODPECKERS IN COASTAL FORESTS OF WASHINGTON

KEITH B. AUBRY,[1] U.S. Forest Service, Pacific Northwest Research Station, Olympia, WA 98512, USA
CATHERINE M. RALEY, U.S. Forest Service, Pacific Northwest Research Station, Olympia, WA 98512, USA

Abstract: Providing adequate habitat for the pileated woodpecker (*Dryocopus pileatus*) is a key component of federal forest management plans in the Pacific Northwest, yet information is extremely limited on characteristics of trees selected by this species for nesting or roosting in coastal forests. We investigated selection by pileated woodpeckers of both individual tree and site characteristics for nesting and roosting in coastal forests, and evaluated the efficacy of current management prescriptions for these woodpeckers on federal lands. From 1990 to 1995, we used call surveys, ground searches, and radiotelemetry to locate 25 nest and 144 roost trees used by 31 adult pileated woodpeckers (16 females, 15 males) in western hemlock (*Tsuga heterophylla*) forests located about 20 km east of the Pacific coast in Washington, USA. Nesting pairs typically excavated nest cavities in different trees each year, and individual birds used an average of 7 different roost trees during the nonbreeding season. Pileated woodpeckers used decadent live trees as often as snags for both nesting and roosting. They selected Pacific silver fir (*Abies amabilis*) for nesting and western redcedar (*Thuja plicata*) for roosting, and selected against western hemlock for both activities. For nesting, pileated woodpeckers used only trees 65–154 cm in diameter at breast height (dbh) but were not selective within this range; for roosting, they selected trees 155–309 cm dbh and selected against trees <125 cm dbh. For both nesting and roosting, pileated woodpeckers selected trees ≥27.5 m tall and selected against trees <17.5 m tall. Decay characteristics of trees used by pileated woodpeckers for nesting differed strongly from those used for roosting. Site characteristics also influenced selection of nest and roost trees by pileated woodpeckers; 0.4-ha plots around nest and roost trees contained a higher diversity of tree species and higher densities of decadent trees ≥20 cm dbh and snags ≥50 cm dbh than availability plots. The Northwest Forest Plan specifies the retention of 1 large, hard snag per 17 ha of harvested forest to provide nest trees for pileated woodpeckers. Our results indicate that providing adequate habitat for pileated woodpeckers in coastal forests of the Pacific Northwest may require a more comprehensive management strategy that also includes provisions for roost trees and that emphasizes retention of both snags and decadent trees, especially those infected with heart-rot decay fungi.

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Key words: *Abies amabilis*, decadent tree, *Dryocopus pileatus*, forest management, heart-rot fungi, nest, Pacific Northwest, Pacific silver fir, pileated woodpecker, roost, snag, *Thuja plicata*, *Tsuga heterophylla*, western hemlock, western redcedar.

Prior to the implementation of the Northwest Forest Plan (NWFP) on federal lands in western Washington and Oregon and portions of northwestern California, USA, during 1994 (U.S. Forest Service and U.S. Bureau of Land Management 1994, Tuchmann et al. 1996), the pileated woodpecker was designated as a management indicator species (MIS) for mature and old-growth forest conditions on 16 of 19 (84%) national forests in the Pacific Northwest Region due to its dependence on large snags and logs for nesting, roosting, and foraging (U.S. Forest Service 1984, 1986). Minimum management requirements specified that habitat areas would be established for pileated woodpeckers in each 5,000 ha of forest. Within each habitat area, large aggregated blocks of mature and old-growth forest and minimum densities of large, hard snags were to be maintained as nesting and foraging habitat for pileated woodpeckers (U.S. Forest Service 1986); neither roosting habitat nor the potential importance of live trees with heartwood decay for nesting were included in these management prescriptions. To evaluate the effectiveness of these habitat areas for maintaining populations of pileated woodpeckers, monitoring of habitat occupancy and population trends also was required (U.S. Forest Service 1982).

The NWFP represents an ecosystem management strategy designed to provide for the long-term viability of northern spotted owl (*Strix occidentalis caurina*) populations, as well as a broad array of other animal and plant species associated with late-successional forests. With the implementation of the NWFP, pileated woodpecker habitat management areas were no longer required on national forests within the range of the northern spotted owl because it was believed that management prescriptions in the NWFP would maintain viable populations of all species associated with late-successional forest conditions

[1] E-mail: kaubry@fs.fed.us

(U.S. Forest Service and U.S. Bureau of Land Management 1994:C-45). The NWFP provides for extensive reserves of late-successional forest, but in many areas, a substantial proportion of federal lands is available for timber harvest (designated as matrix lands in the NWFP). Although harvest prescriptions on matrix lands include standards and guidelines for snag and green-tree retention in harvest units (U.S. Forest Service and U.S. Bureau of Land Management 1994), the extent to which these prescriptions will provide adequate nesting, roosting, or foraging habitat for pileated woodpeckers in coastal forests has not been evaluated empirically.

Information on the characteristics of trees used by pileated woodpeckers for nesting and roosting in coniferous forests of the Pacific Northwest is limited, especially in coastal forests. Large data sets are available only from Douglas-fir (*Pseudotsuga menziesii*) forests in southcentral British Columbia (n = 20 nest trees; Harestad and Keisker 1989), western larch (*Larix occidentalis*)–Douglas-fir forests in northwestern Montana (n = 97 nest trees and 40 roost trees; McClelland and McClelland 1999), and grand fir (*Abies grandis*)–Douglas-fir forests in northeastern Oregon (n = 105 nest trees and 23 roost trees; Bull 1987; n = 36 nest trees and 123 roost trees; Bull et al. 1992). However, data on trees used by pileated woodpeckers for nesting or roosting within the range of the northern spotted owl in western Washington and Oregon are limited to the results of 3 descriptive studies in Douglas-fir forests in the Coast Range of western Oregon: Mannan et al. (1980) described 7 nest trees; Mellen (1987) and Mellen et al. (1992), 15 nest and 18 roost trees; and Nelson (1988), 6 nest trees. No information is available on nest or roost trees used by pileated woodpeckers in coastal forests dominated by western hemlock or Sitka spruce (*Picea sitchensis*).

Because forest components for pileated woodpeckers vary geographically, extrapolating information from 1 region to another may be misleading (McClelland and McClelland 1999). Detailed information on the habitat relations of pileated woodpeckers in coastal forests of the Pacific Northwest is needed to design effective management strategies within the range of the northern spotted owl. Our objectives were to (1) describe the characteristics of nest and roost trees selected by pileated woodpeckers in coastal forests of Washington, (2) identify physiographic and vegetative site characteristics selected by pileated woodpeckers for nesting and roosting, and (3) evaluate the efficacy of management provisions in the NWFP for providing nesting and roosting habitat for pileated woodpeckers in coastal forests of the Pacific Northwest.

STUDY AREA

We conducted this study on the Olympic Peninsula in northwestern Washington, USA, 20 km from the Pacific coast on the west slope of the Olympic Mountains. Our study area was located near the town of Forks in Clallam and Jefferson counties on lands managed by the U.S. Forest Service (Olympic National Forest), Washington Department of Natural Resources (Olympic Experimental State Forest), and National Park Service (Olympic National Park). The last ownership was limited to a narrow strip of the park 725 ha in extent on the eastern edge of the study area. The remainder of the study area was managed for timber production. Clearcutting was the primary timber harvest system used on both federal and state lands.

The study area comprised 9,350 ha of highly dissected, mountainous terrain ranging from 92 to 488 m in elevation with a mean annual precipitation of 305 cm (Henderson et al. 1989). Western hemlock was the predominant tree species in the study area, but Pacific silver fir and western redcedar were important codominant species in many locations. Due to moist environmental conditions resulting from maritime climatic influences, Douglas-fir was rare in the study area, except where it had been planted for reforestation after clearcutting. Red alder (*Alnus rubra*) was a common early seral species that persisted after canopy closure on some of the wetter sites. Sitka spruce is restricted to a narrow zone adjacent to the coast and was uncommon in the study area. Both historic wind events and timber harvesting have influenced forest conditions and landscape patterns in the study area. During 1921, a hurricane-force windstorm impacted an area 96 km long and 24–32 km wide on the Olympic Peninsula (Boyce 1929). Within the study area, stands impacted by the storm (1921-blow stands) were characterized by naturally regenerated forests about 75 yr old with large, residual live trees and snags (see Morrison 1990:7). About 47% of the study area was unmanaged late-successional forest, 20% second-growth forest <35 yr old, 13% recent clearcuts, 11% 1921-blow stands, and 9% hardwoods or nonforested habitats.

METHODS

Locating Nest and Roost Trees

To locate areas occupied by breeding pairs of pileated woodpeckers, we conducted call surveys during March and April from 1990 to 1993 using techniques modified from Bull et al. (1990). We did not need to conduct call surveys during 1994 or 1995 because at least 1 member of each pair was alive and radiomarked during those years. Because taped pileated woodpecker calls could be heard at least 0.4 km away, we used a combination of logging roads and off-road transects spaced ≤0.8 km apart to obtain complete coverage of the study area. We began walking survey routes 0.5 hr after sunrise, stopping at 300-m intervals to listen for pileated woodpecker calls. If we heard no pileated woodpeckers after 1 min, we played a taped pileated woodpecker call and drum at 30-sec intervals, repeated 7 times or until we heard a response. We marked the locations of all pileated woodpecker responses on a 7.5-min U.S. Geological Survey topographic map. To locate nest trees, we systematically searched each activity area for fresh cavity chips (Bull et al. 1990) at the base of snags and live trees with dead or broken tops (hereafter referred to as decadent trees). These techniques enabled us to locate all breeding pairs in the study area.

We trapped adult birds in the nest cavity after the young were at least 2 days old using board traps (Bull and Pedersen 1978) or nooses (Cooper et al. 1995). We also captured several nonbreeding adults at roost trees using nooses or mist nets. We attached 12-g AVM transmitters with a 9-month battery life (1991) or 9-g Holohil transmitters with a 12-month battery life (all subsequent years) to captured birds with a backpack harness made of tubular Teflon ribbon about 5 mm (3/16 in) wide. We tracked birds year-round. For each individual, we attempted to locate 2 roost trees per month spaced at least 1 week apart. We located roost trees by radiotracking birds after dark and isolating the radio signal to a single tree. We verified roost trees and the location of roost-cavity openings by observing birds leaving in the morning. We followed individual birds until they died or until we removed the transmitters during spring 1995.

Nest and Roost Trees and Site Characteristics

For each nest and roost tree, we recorded species; tree condition (live or dead); top condition (single or multiple top, intact or broken, live or dead); location of the cavity opening in the canopy (above, within, or below the canopy); and location of the cavity opening on the bole (above or below the highest live limb). We measured dbh to the nearest centimeter, tree height and height of the cavity opening to the nearest meter, and aspect of the cavity opening to the nearest degree. Commonly used decay classes for snags of Douglas-fir (Cline et al. 1980) and ponderosa pine (*Pinus ponderosa*; Thomas et al. 1979) failed to adequately describe decay characteristics for western hemlock, Pacific silver fir, or western redcedar. Consequently, to characterize different stages of snag decay, we recorded top condition, percent bark remaining, number of dead limbs, and presence of small twigs and dead foliage.

We hypothesized that selection of nest and roost trees by pileated woodpeckers may be influenced by the physiographic characteristics of the site or by the abundance of snags, decadent trees, or logs near the nest or roost tree. Such trees and snags may provide alternative structures if nest or roost trees become unsuitable, and snags or logs near a nest or roost tree may provide foraging sites that are easily defended and can be accessed with relatively low energetic costs. To investigate these hypotheses, we quantified habitat characteristics likely to be important to pileated woodpeckers in a 0.4-ha (1-acre) circular plot around each nest and roost tree. Although previous researchers have used smaller plot sizes to describe site characteristics around pileated woodpecker nest trees or to quantify the availability of potential nest trees (e.g., Bull 1987: 0.1 ha; Harestad and Keisker 1989: 0.02 ha), field evaluations showed that a larger plot was needed to obtain a representative sample of large snags and decadent trees in our study area.

In each plot, we recorded slope, aspect, and elevation. For all snags and decadent trees ≥20 cm dbh and ≥1 m tall, we recorded tree species, tree condition, and top condition, measured dbh to the nearest centimeter, and estimated tree height to the nearest 5 m. For snags, we also recorded percent bark remaining, number of dead limbs, and presence of small twigs and dead foliage. We visually estimated the percent contribution of each tree species to the total canopy cover above the plot. We used a random azimuth to establish a 71.4-m-diameter line transect in each plot, and used the line-intercept method to sample logs ≥20 cm in diameter at the large end and ≥1 m in length that were in the early stages of decay (log decay classes 1–3; Sollins 1982). We did not sample severely decayed or smaller logs because our field observations indicated that these structures were rarely used by pileated woodpeckers for foraging. For each log, we recorded species and decay class, and measured diameter at the large end to the nearest centimeter and length to the nearest meter.

We sampled habitat available to pileated woodpeckers for nesting and roosting by randomly locating 261 0.4-ha circular plots on a series of transects oriented due north and spaced 800 m apart throughout the study area. We established the location of the transect grid by randomly selecting a distance <400 m from the eastern boundary of the study area to the first transect. On each transect, we established the first plot center by randomly selecting a distance <400 m from the northern end of the transect. We established subsequent plots at 400-m intervals along the transect using a compass and measuring tape until we reached the southern boundary of the study area. We measured habitat characteristics in each plot as described previously for plots around nest and roost trees. Of the 261 availability plots, 209 were in closed-canopy stands and 52 were in grass–forb, shrub, or open sapling–pole stand conditions (Hall et al. 1985). Because pileated woodpeckers do not nest or roost in precanopy conditions, we included only closed-canopy plots in analyses of resource selection.

Statistical Analyses

To test the hypotheses that aspects of nest- and roost-cavity openings did not differ from a random distribution and did not differ from each other, we used Kuiper's 1-sample (K) and 2-sample (k) tests for circular data (Batschelet 1981:112). To maintain an experiment-wide α level of 0.05, we used $\alpha = 0.01$ to identify statistical significance in each test (Miller 1985:67).

To test the hypotheses that species, dbh, and height of snags and decadent trees used by pileated woodpeckers for nesting or roosting did not differ from availability, we used chi-square tests of homogeneity (Jelinski 1991). We used 30-cm intervals for dbh classes and 10-m intervals for height classes; however, to ensure that all cells had expected values >0, we combined the largest dbh and height values into single classes (215–309 cm and 37.5–67.4 m, respectively). To ensure that analyses of resource selection were biologically meaningful, we limited chi-square analyses to resource categories for which we had documented use by pileated woodpeckers and that were available for them to select. Accordingly, we limited statistical tests to dbh and tree-height categories ≥65 cm and ≥7.5 m, respectively, because pileated woodpeckers clearly used smaller size classes of trees less than expected for both nesting and roosting in our study area and statistical tests were unnecessary (see Cherry 1998). None of the nest trees and only 2% (3/144: 37, 51, and 52 cm dbh) of the roost trees we found were 20–65 cm dbh, yet 46% of snags and decadent trees sampled in availability plots were in this size range. In addition, we split our analysis of roost tree species selection into 2 analyses based on dbh because Pacific silver fir rarely grows larger than 155 cm dbh in our study area, but both western hemlock and western redcedar reach diameters >155 cm.

Because we sampled the availability of snags and decadent trees in a series of 0.4-ha plots distributed throughout the study area, data within plots may not be independent. To ensure that P-values obtained from chi-square tests reflected the sampling structure of our availability data, we used restricted bootstrapping techniques as recommended by Fortin and Jacquez (2000) for analyzing data that are spatially autocorrelated. If results of chi-square tests were significant (we used $\alpha = 0.007$ for individual tests to maintain an experiment-wide α level of 0.05), we identified tree species or size classes that were used significantly more or less than expected by examining adjusted standardized residuals, and using a minimum residual distance of ±2.00 to approximate statistical significance at $\alpha = 0.05$ (Haberman 1973, Kennedy 1983:64).

We used logistic regression analysis to identify habitat characteristics that distinguished sites used by pileated woodpeckers from availability plots. For this analysis, we pooled sites used by pileated woodpeckers for nesting and roosting because 40% of the nest trees we located were eventually used as roosts, indicating that sites selected for nesting and roosting were not mutually exclusive. We began by identifying a subset of habitat variables that were useful for distinguishing used from availability plots and were not strongly intercorrelated (Spearman correlation coefficients <0.50). To construct the final logistic regression model, we used variable-selection and model-building strategies suggested by Hosmer and Lemeshow (1989).

Our analyses of resource selection correspond to study design 2 described by Thomas and Taylor (1990), whereby data on resource use are pooled among study animals, and resource availability is considered to be the same for all individuals. Results of statistical tests therefore provide inferences about resource selection by the population of birds that occupied our study area. This design is appropriate, and assumptions of independence of samples and equal availability of resources among birds were generally met for the following reasons: (1) our field techniques enabled us to radiomark all breeding pairs within the study area each year; (2) we determined the study area boundary based on areas used by radiomarked birds (see Jones 2001); (3) we used equal sampling effort throughout the study area to locate roosts and to sample available habitat; (4) the species composition and structure of forests were similar throughout the study area; (5) for each radiomarked bird, all but a few roost trees were located at least 4 days apart; (6) we included each nest and roost tree once in our analyses, even if it was reused by the same or by a different individual; and (7) we excluded 1 nest and 16 roost trees from analyses of resource selection because they were <65 cm dbh, or were in trees with live tops (which we did not sample in availability plots), or were outside of the area we sampled with availability plots.

We conducted most of our analyses using SPSS 10.0 for Windows. Two exceptions were Kuiper's tests for circular data, which we calculated by hand, and the restricted bootstrapping analysis, which we conducted using a SAS program developed for this analysis by K. Hyer (U.S. Forest Service, Portland, Oregon, USA).

Table 1. Characteristics of nests and roosts used by pileated woodpeckers in coastal forests of Washington, USA, 1990–1995.

Variable	Nest trees		Roost trees	
	n	%	*n*	%
Tree species				
Western hemlock	17	68	75	52
Pacific silver fir	7	28	7	5
Western redcedar	0	0	61	42
Red alder	1	4	0	0
Douglas-fir	0	0	1	1
Snag: top condition				
Single top, intact	1	4	2	1
Single top, broken	11	44	65	45
Multiple tops[a]	1	4	5	4
Live tree: top condition				
Single live top, intact	0	0	5	4
Single dead top, intact	1	4	10	7
Multiple tops[b]	0	0	19	13
Single dead top, broken	11	44	38	26
Canopy position of cavity opening[c]				
Above the canopy	5	18	11	8
Within the canopy	21	78	84	58
Below the canopy	1	4	43	30
Unknown[d]	0	0	6	4
Placement of cavity opening[c]				
Bole of snag	15	56	72	50
Bole of live tree above highest live limb	12	44	19	13
Bole of live tree below highest live limb	0	0	50	35
Unknown[d]	0	0	3	2

[a] Can be intact, broken, or both.
[b] Can be live, dead, or both; can be intact, broken, or both.
[c] n = 27 for nest cavities (2 trees were used for nesting in consecutive years).
[d] Roost trees were verified but observers could not determine the exact location of cavity openings used.

RESULTS

Nest Trees

We trapped and radiomarked 31 adult pileated woodpeckers (16 females, 15 males) and located 27 nest cavities in 25 trees from 1990 to 1995. Two trees were used for nesting in consecutive years, but both pairs excavated a new cavity each year. Three tree species were used for nesting: 68% western hemlock, 28% Pacific silver fir, and 4% red alder (Table 1). Pileated woodpeckers used equal numbers of snags and decadent trees for nesting, but proportions varied by species: 65% (11/17) of western hemlock nest trees were decadent, whereas 86% (6/7) of Pacific silver fir nest trees were snags. All but 2 of the nest trees had broken tops. Most snags used for nesting (10/13) were in the early stages of decay with intact bark and remnant limbs with small twigs or dead foliage still present. Nest trees used by pileated woodpeckers averaged 101.2 cm dbh and 39.3 m in height; the smallest tree used was a red alder snag 65 cm dbh and 17 m tall (Table 2).

We found no evidence that aspects of nest-cavity openings differed from a random distribution. The average height of nest openings was 35.3 m, and none was located below 15 m in height (Table 2). Most nest openings (78%) were located within the canopy, and only 1 was excavated below the canopy (Table 1). All nest openings in decadent trees (n = 12) were located several meters above the highest live limb ($\bar{x}$ = 4.6 m, range = 2.5–8.0 m).

Table 2. Diameter at breast height (dbh) and height of nest, roost, and available trees; and tree diameter and height at cavity openings used by pileated woodpeckers in coastal forests of Washington, USA, 1990–1995.

Variable	Nest trees (n = 25)			Roost trees (n = 144)			Available trees (n = 1,815)[a]		
	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
dbh (cm)	101.2	20.2	65–154	149.0	57.9	37–309	68.7	40.4	20–372
Height (m)	39.3	10.4	17–56	36.5	10.7	11–63	12.6	8.7	5–65
Diameter at cavity opening (cm)[b]	52.0	11.5	31–81	78.3	32.9	28–185	–	–	–
Height at cavity opening (m)[c]	35.3	9.0	15–52	23.0	9.4	3–46	–	–	–

[a] Snags and decadent trees ≥20 cm dbh and ≥5 m tall.
[b] n = 27 for nest cavities (2 trees were used for nesting in consecutive years); n = 132 for roost cavities (measurements were not taken at 12 roost trees).
[c] n = 27 for nest cavities; n = 134 for roost cavities (measurements were not taken at 10 roost trees).

Roost Trees

We located 144 different roost trees for 27 adult birds (15 females, 12 males) based on 474 observations of roosting birds from 1991 to 1995. With the exception of a single observation of 2 birds (a pair) roosting in the same tree on the same night, pileated woodpeckers roosted alone in tree cavities at night during all months of the year. During trapping activities, we inspected cavities in 20 roost trees; all contained extensive hollows created by heartwood decay. We determined the nature of entrance holes for 137 roost trees (7 were obscured by foliage); of these, 80% were openings excavated by pileated woodpeckers and 20% were natural openings (cracks, knotholes, or open top). Many roost trees were used by more than 1 individual during the study (22%), and most (58%) were used multiple times by the same bird. During the nonbreeding period (1 Jul–28 Feb), pileated woodpeckers used an average of 7.2 different roost trees per individual (n = 13, range = 4–11). We excluded roost trees used during the breeding and nesting season (1 Mar–30 Jun) from this calculation because male pileated woodpeckers begin roosting in the nest cavity prior to egg laying during mid- to late April, and continue roosting in the nest at night until the young fledge in mid- to late June.

Most trees used by pileated woodpeckers for roosting were either western hemlock (52%) or western redcedar (42%; Table 1). As with nest trees, pileated woodpeckers used equal numbers of snags and decadent trees for roosting but the proportion varied by species: 68% (51/75) of western hemlock and 86% (6/7) of Pacific silver fir roost trees were snags, whereas 77% (47/61) of western redcedar roost trees were living. Most snags used for roosting were in later stages of decay than those used for nesting; only 27% (19/71) of roost snags had intact bark and remnant limbs with small twigs or dead foliage still present, compared to 77% for nest snags. Roost trees had a variety of top conditions; most (71%) had broken tops, but 17% had multiple tops and 12% had single, intact tops (Table 1). Roost trees averaged 149.0 cm dbh and 36.5 m in height; the smallest diameter tree used for roosting was a decadent western hemlock 37 cm dbh, and the shortest tree used was a western hemlock snag 11 m tall (Table 2).

We found no evidence that aspects of roost-cavity openings differed from a random distribution or that they differed from aspects of nest openings. The average height of roost openings was 23.0 m, and none was located below 3 m in height (Table 2). Thirty percent of roost openings were located below the canopy and, in decadent trees, most roost openings (50/69) were located below the highest live limb (Table 1).

Selection of Nest and Roost Trees and Site Characteristics

Pileated woodpeckers were selective in their use of tree species for both nesting and roosting. Pileated woodpeckers used Pacific silver fir for nesting and western redcedar for roosting more than expected (i.e., selected), and western hemlock less than expected (i.e., selected against) for both nesting and roosting (Fig. 1). Pileated woodpeckers also were selective in their use of tree heights, selecting trees ≥27.5 m tall, and selecting against trees <17.5 m tall for both nesting and roosting. Pileated woodpeckers only nested in trees 65–154 cm dbh but were not selective within this range. For roosting, however, pileated woodpeckers selected trees 155–309 cm dbh, used trees 125–154 cm dbh in proportion to availability, and selected against trees 65–124 cm dbh.

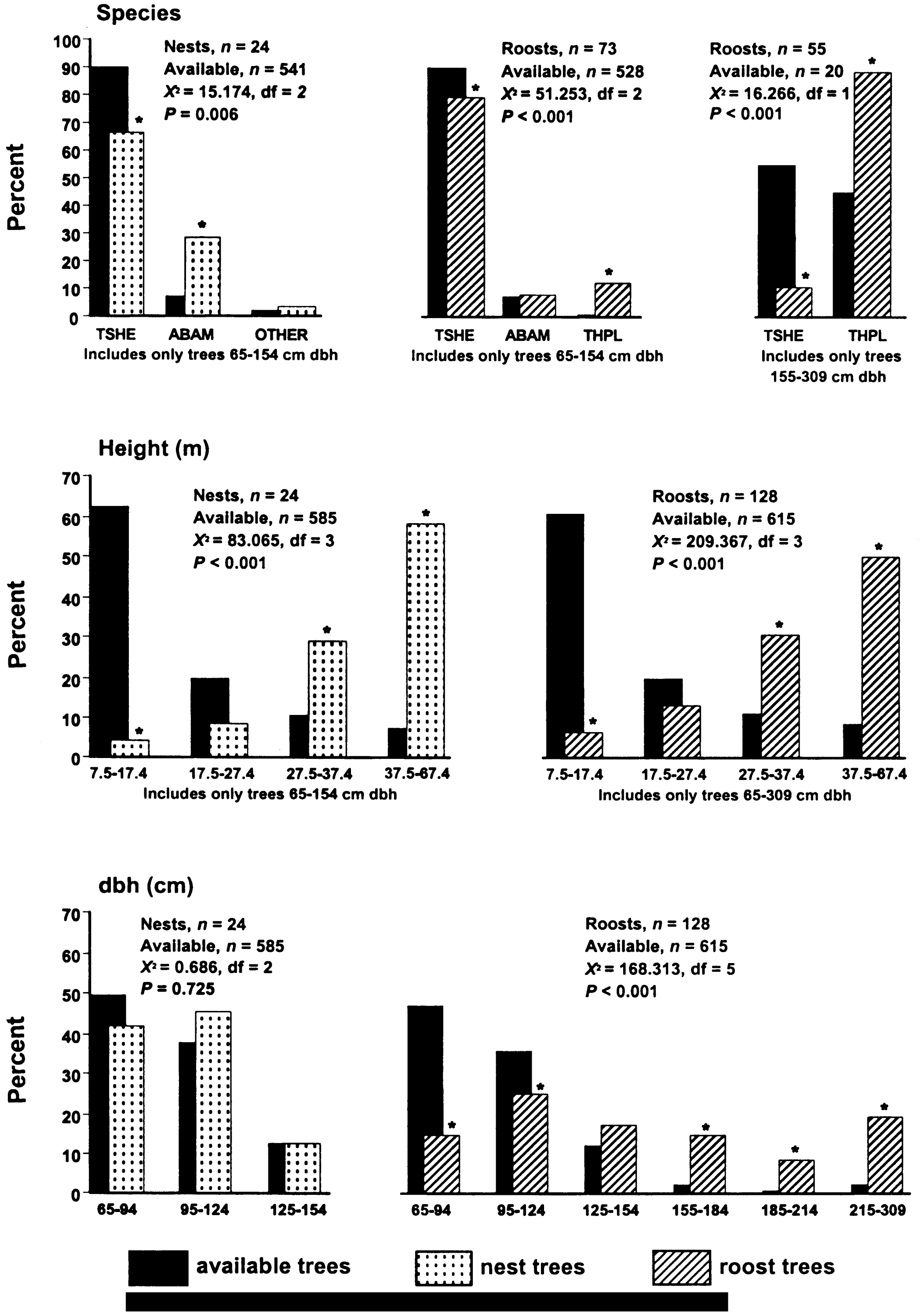

Fig. 1. Frequency distributions and chi-square tests of homogeneity comparing characteristics of snags and decadent trees used by pileated woodpeckers for nesting and roosting with available snags and decadent trees. Abbreviations for tree species: TSHE = western hemlock, ABAM = Pacific silver fir, THPL = western redcedar, OTHER = red alder, Douglas-fir, and Sitka spruce. Asterisks indicate categories for which adjusted standardized residuals were >±2.0.

Table 3. Continuous physiographic and vegetation variables for availability plots (n = 209) and plots used for nesting and roosting (n = 154) by pileated woodpeckers in coastal forests of Washington, USA, 1990–1995.

	Availability plots			Use plots		
Variable	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
Elevation (m)	255	94	64–518	261	93	98–530
Slope (degrees)	23	13	0–65	22	13	0–55
No. snags and decadent trees ≥20 cm dbh and 1–7.4 m tall/plot[a]	15.0	9.0	0–66	20.5	9.7	1–52
No. snags 20–49 cm dbh and ≥7.5 m tall/plot	1.8	2.3	0–13	2.5	2.8	0–15
No. snags ≥50 cm dbh and ≥7.5 m tall/plot[b]	3.3	3.1	0–15	7.0	3.4	0–18
No. decadent trees ≥20 cm dbh and ≥7.5 m tall/plot[b]	0.3	0.8	0–6	3.0	2.9	0–18
Percent western hemlock snags and decadent trees/plot	65	37	0–100	74	23	0–100
No. tree species/plot[b, c]	1.8	0.8	0–4	2.4	0.8	1–5
No. logs ≥20 cm diameter and ≥1 m long/ha	261.8	210.8	0–1,225	320.2	216.2	0–1,016
Log volume (m^3/ha)[a]	105.0	82.4	0–441	159.1	117.7	0–582
Average log diameter (cm)	50.0	0.99[d]	21–100	49.1	0.97[e]	24–115
Average log length (m)[a]	10.6	0.36[d]	2–30	12.4	0.40[e]	3–29

[a] Variables considered in the modeling process but not used in the final logistic regression model.
[b] Variables used in the final logistic regression model.
[c] Includes all snags and decadent trees ≥20 cm dbh and ≥1 m tall.
[d] Standard error; n = 200.
[e] Standard error; n = 152.

Among the 17 habitat variables we considered for logistic regression analysis, we chose 7 for inclusion in the modeling process (Tables 3, 4). Three variables were included in the final logistic regression model. Compared with availability plots, those used by pileated woodpeckers for nesting or roosting had a higher diversity of tree species and higher densities of decadent trees and large snags (Table 5). The probability that a site would be used for nesting or roosting increased by a factor of 3 for each additional decadent tree/0.4 ha, a factor of 2 for each additional tree species/0.4 ha, and a factor of 1.3 for each additional large snag/0.4 ha.

DISCUSSION

Selection of Nest Trees

Pileated woodpeckers occupy many coniferous and deciduous forest types, and use a variety of tree species for nesting (Bull and Jackson 1995). Several studies in western coniferous forests have shown, however, that pileated woodpeckers are selective in their choice of tree species for nesting. In our study, pileated woodpeckers selected Pacific silver fir and selected against western hemlock for nesting; use of other species was rare and in proportion to availability (Fig. 1). Pileated woodpeckers selected western larch and selected against Douglas-fir for nesting in northwestern

Table 4. Categorical physiographic and vegetation variables for availability plots (n = 209) and plots used for nesting and roosting (n = 154) by pileated woodpeckers in coastal forests of Washington, USA, 1990–1995.

Variable	Availability plots (%)	Use plots (%)
Plot aspect		
NW-NE	40	39
E	12	12
SE-SW	40	39
W	8	10
Pacific silver fir snags and decadent trees ≥20 cm dbh and ≥7.5 m tall[a]		
Absent	68	37
Present	32	63
Percent live Pacific silver fir in the canopy[b]		
0	39	16
1–4	9	22
5–14	25	25
≥15	27	37
Percent live western hemlock in the canopy[b]		
<60	22	23
60–84	25	29
85–94	21	18
≥95	32	30
Live western redcedar in the canopy		
Absent	88	60
Present	12	40

[a] Variables considered in the modeling process but not used in the final logistic regression model.
[b] Categories based on quartiles for availability data.

Table 5. Logistic regression model distinguishing availability plots (response = 0) and pileated woodpecker nest and roost plots (response = 1) in coastal forests of Washington, USA, 1990–1995. The Wald statistic for each of the habitat variables was significant at $P < 0.001$. –2 log likelihood = 265.041, model $\chi^2 = 229.818$, df = 3, $P < 0.001$.

Variable	β	SE (β)	Odds ratio[a]	95% CI for odds ratio
No. decadent trees[b]/plot	1.067	0.149	2.906	2.170–3.891
No. species[c]/plot	0.747	0.206	2.111	1.409–3.162
No. large snags[d]/plot	0.281	0.049	1.325	1.205–1.457
Constant	–4.438	0.571		

[a] Odds ratio = *Exp* (β); the factor by which the odds that a plot will be used for nesting or roosting change for every 1-unit increase in the independent variable.
[b] ≥20 cm dbh and ≥7.5 m tall.
[c] All snags and decadent trees ≥20 cm dbh and ≥1 m tall.
[d] ≥50 cm dbh and ≥7.5 m tall.

Montana (McClelland and McClelland 1999); selected ponderosa pine and western larch and selected against lodgepole pine (*Pinus contorta*), Douglas-fir, and grand fir in northeastern Oregon (Bull 1987); and nested exclusively in trembling aspen (*Populus tremuloides*) in forests dominated by Douglas-fir in southcentral British Columbia, Canada (Harestad and Keisker 1989). Although Douglas-fir was selected against in all of these studies, it was commonly used for nesting in western Oregon and on southern Vancouver Island in British Columbia (Mellen 1987, Nelson 1988, Hartwig 1999). These widely varying observations indicate that selection of tree species by pileated woodpeckers is not determined only by the physical characteristics of available species.

Pileated woodpeckers also are selective in their choice of tree sizes for nesting because nest trees must be of sufficient diameter to contain their large nest cavity. The 25 nest trees we found in this study had the largest mean diameter and height (Table 2) reported for pileated woodpeckers in North America (compare Conner et al. 1975, Brawn et al. 1984, Bull 1987, Harestad and Keisker 1989, Mellen et al. 1992, McClelland and McClelland 1999). We believe that trees used by pileated woodpeckers for nesting in western hemlock forests are bigger and taller than those in other forest types simply because the coastal forests we studied have larger trees to select from. Although the nest trees in our study area had a larger mean dbh than those reported elsewhere, tree diameters at the cavity were within the range of those found in other studies (Table 2; Bull 1987, Mellen 1987, Nelson 1988). Selection by pileated woodpeckers for nesting in the tallest trees available also may reflect the preponderance of nests in decadent trees and recently dead snags, both of which retain much of their original height.

In forest types with a relatively narrow range of tree sizes, pileated woodpeckers generally select the largest trees available for nesting (Bull 1987, Harestad and Keisker 1989, McClelland and McClelland 1999). These observations have led to the assumption that, above a minimum dbh (e.g., 50.8 cm in northeastern Oregon [Thomas et al. 1979] and 63.5 cm in western Washington and Oregon [Neitro et al. 1985, U.S. Forest Service and U.S. Bureau of Land Management 1994]), all potential nest trees are equally suitable for pileated woodpeckers. Our results suggest, however, that in forests with a wide range of available tree sizes, very large trees may not provide optimal conditions for nesting. Although larger trees were available, pileated woodpeckers nested only in trees 65–154 cm dbh (Fig. 1, Table 2). Pacific silver fir does not grow much larger than the range of tree diameters used for nesting; however, western hemlocks >154 cm dbh were used for roosting, but not for nesting (Fig. 2). Harris (1982) found a similar pattern in California, where pileated woodpeckers selected nest trees that were intermediate in size, and selected against both the smallest and largest size classes. Pileated woodpeckers may select this range of tree diameters for nesting be-

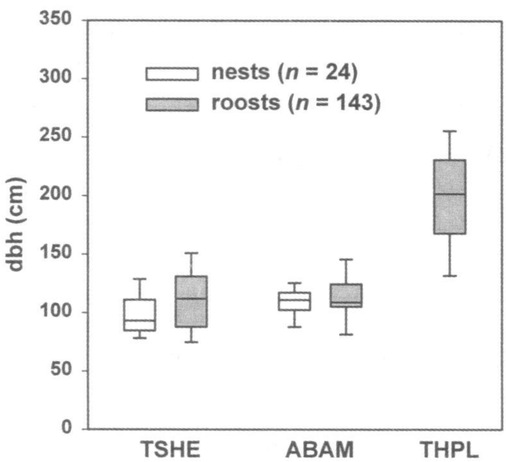

Fig. 2. Box plots of diameter at breast height (dbh) values for pileated woodpecker nest and roost trees by species (TSHE = western hemlock, ABAM = Pacific silver fir, THPL = western redcedar). The horizontal line within the box is the median, the box includes 50% and the terminal bars include 80% of the values around the median; outliers are not shown. Two trees were not included: 1 nest in a red alder and 1 roost in a Douglas-fir.

cause they can more easily detect potential predators at the nest, or perhaps the thick bark of very large trees hinders their ability to detect the requisite decay characteristics for nest excavation.

Pileated woodpeckers also are selective in their choice of nest trees according to the nature and extent of decay in both the heartwood and sapwood. Many researchers have reported that pileated woodpeckers select nest trees that have heartwood softened by decay to facilitate excavation, and sound sapwood for structural support (e.g., Conner et al. 1975, 1976; Harris 1983; Harestad and Keisker 1989; McClelland and McClelland 1999). Although pileated woodpeckers are strong excavators (Bull 1987), for most tree species, digging out cavities in undecayed heartwood probably is too energetically demanding (Conner et al. 1976, Harris 1983), and heartwood in the final stages of decay does not have the structural integrity to support a pileated woodpecker cavity. According to previous studies, pileated woodpeckers in western coniferous forests typically nest in snags in the early stages of decay (Madsen 1985, Bull 1987, Mellen 1987, Nelson 1988, McClelland and McClelland 1999), presumably because such structures are most likely to provide optimal conditions for nesting. Decay classes of snags (e.g., Cline et al. 1980) only describe external characteristics of dead trees, however, and do not necessarily reflect differences in the presence, extent, or stage of heartwood decay. Among 105 pileated woodpecker nest trees found in northeastern Oregon, all but 1 were snags (Bull 1987). In western Montana, 81% (78/96) of nest trees were snags (McClelland and McClelland 1999). In coastal forests of Washington, however, pileated woodpeckers excavated nest cavities as often in decadent trees (12/25, including 11 with broken tops and 1 with a dead, intact top) as in snags (13/25). Although half of the nests we found were in decadent trees, such structures were extremely rare in our study area. In our sample of available habitat structures 65–154 cm dbh and ≥7.5 m tall, 94% were snags and only 6% were decadent trees. Thus, contrary to previous findings from western coniferous forests, it appears that, in our study area, optimal conditions for pileated woodpecker nest sites are more likely to occur in decadent trees than in snags. We speculate that this apparent selection for live, broken-top trees for nesting by pileated woodpeckers in our study area reflects a higher prevalence of suitable heartwood decay conditions in decadent trees than in snags.

Heart-rot decay fungi only infect living trees, and only when top or limb breakage, lightning strikes, frost cracks, or injury from the windthrow of nearby trees expose the heartwood to infection (Wagener and Davidson 1954, Bull et al. 1997). Determining the presence or absence of heartwood decay in the field can be problematic, however, because a lack of fungal conks does not necessarily mean that heartwood decay is absent. Some heart-rot fungi produce few fruiting bodies and may only do so after extensive decay has occurred (Boyce 1961:363, Farr et al. 1976, Manion 1991:269). Furthermore, examining excavated chips collected on the ground below nest cavities may be unreliable because incipient decay may not be visible even though the wood has been weakened (Boyce 1961:345). However, available evidence indicates that the presence of heartwood decay in living trees can be inferred reliably from the presence of broken tops. Because broken tops expose a large surface area of heartwood, they provide a particularly favorable site for infection by heart-rot fungi (Wagener and Davidson 1954, Boyce 1961:364). Broken tops also may occur after the bole has been weakened from an infection of heart-rot fungi that was initiated by a trunk wound or broken branch. Whether top breakage occurs before or after infection, live western hemlock and Pacific silver fir trees with broken tops are almost certain to be infected by heart-rot fungi (Kimmey 1964, Farr et al. 1976, Filip et al. 1984). Additionally, 2 of the live, broken-top nest trees we found had fruiting bodies of a white trunk rot on the underside of branch stubs a few meters above the cavity openings. These fruiting bodies were identified as belonging to a species complex that includes *Phellinus hartigii*, a common heart-rot of old-growth western hemlock trees on the western Olympic Peninsula (D. Shaw, University of Washington, personal communication).

Unlike live trees, snags with broken tops have not necessarily been decayed by heart-rot fungi, because tops may break off after death when the tree is no longer susceptible to infection. However, we also identified fruiting bodies of the same white trunk rot on 2 western hemlock snags containing nest cavities, and cavity chips from both trees were visibly decayed. Tree diameter and age data from the Olympic Peninsula indicate that the Pacific silver fir nest trees we found during this study were >300 yr old (Filip et al. 1984). Although we did not verify infection by heart-rot fungi in these trees, old-growth Pacific silver fir trees are so susceptible to infection by heart-rot fungi (Hepting 1971, Burns and Honkala 1990) that it is virtually certain that the broken-top snags used for nesting in our study area had heartwood decay (G. Filip, Oregon State University, personal communication).

Our results support previous assertions regarding the importance of heartwood decay for selection of nest trees by pileated woodpeckers. However, we question the assumption that, in each locality, the tree species pileated woodpeckers select for nesting are static and determined solely by differences in the physical characteristics of available species. We believe that species selected for nesting will vary if the preponderance of large trees in the early stages of heartwood decay shifts among species. In general, older, suppressed, or otherwise stressed trees are less capable of resisting infection by heart-rot decay fungi than are younger, healthier trees (Manion 1991:272). In our study area, Pacific silver fir occurs at the lower limit of its elevation range and grows in stands dominated by western hemlock. In southwestern Washington, intraspecific competition and low elevation were identified as stress factors contributing to the decline of Pacific silver fir trees impacted by tephra from the eruption of Mount St. Helens (Segura 1991). We suspect that these environmental stress factors, in conjunction with the extreme susceptibility of old Pacific silver fir to infection by heart-rot fungi, may result in proportionately more suitable nest sites in Pacific silver fir than in western hemlock.

Lastly, pileated woodpeckers require nest sites that are easy to access and defend from potential predators. Although most nest trees had some remaining limbs or branch stubs, there were few large branches near nest cavities, and all nests in decadent trees were several meters above the highest live limbs. Numerous limbs close to the cavity opening may hinder the ability of adult birds to fly in and out of the nest and may interfere with the fledging of young. Tree squirrels are a potential nest predator of pileated woodpeckers (Bull and Jackson 1995). Our field observations suggest that adult birds can more readily defend the nest cavity from predators if there are few branches near the cavity.

Selection of Roost Trees

The larger mean diameter of roost trees compared to nest trees (Table 2) was due primarily to selection of very large western redcedars for roosting (Fig. 2). In both intermediate and large diameter classes, pileated woodpeckers selected western redcedar and selected against western hemlock for roosting (Fig. 1). As with nest trees, selection for 1 species over another for roosting probably reflects differences in the prevalence of infection by heart-rot fungi and the process of heartwood decay among available species. In northeastern Oregon, pileated woodpeckers typically roosted in large-diameter live or dead trees with a large, hollow interior created by late stages of heartwood decay (Bull et al. 1992); pileated woodpeckers selected grand fir for roosting, but selected against it for nesting (Bull 1987, Bull et al. 1992). The extensive use of grand fir for roosting in northeastern Oregon was attributed to its greater propensity to form large, hollow chambers in the bole than other available species (Bull et al. 1992). We believe this characteristic also applies to western redcedar in coastal Washington.

Old western redcedars are reported to have a high prevalence of infection by heart-rot fungi (Buckland 1946). All redcedar roosts we examined had large hollows created by heartwood decay. To identify the heart-rot fungi that may be responsible for creating roost cavities in western redcedar, Parks et al. (1997) cultured cores taken from 10 large (200–300 cm dbh) decadent trees that pileated woodpeckers had used for roosting in our study area. All had decayed heartwood, and 8 were infected with *Oligoporus sericeomollis* (= *Poria asiatica*); a brown, cubical heart-rot that, in the late stages of decay, forms a rot column that can extend >25 m within the bole of the tree (Buckland 1946). In both our study area and in northeastern Oregon (Bull et al. 1992), the tree species selected by pileated woodpeckers for roosting was selected against for nesting. Thus, it appears that certain combinations of tree hosts and fungi produce conditions that are suitable for roosting but not for nesting.

All nest cavities we found had been excavated via a single opening into heartwood that appeared to be softened by early stages of decay. In contrast, roost cavities typically had multiple openings, both excavated and natural, that accessed hollows created by late stages of heartwood decay. Pileated woodpeckers probably use hollow trees for roosting because the time and energy demands of excavating multiple cavities for roosting would be too great (Bull et al. 1992); in addition, a hollow with multiple openings provides more escape routes from predators (Bull and Jackson 1995). In our study area, adult birds used an average of 7 roost trees (range = 4–11) during the 9-month nonbreeding period. This agrees closely with findings by Bull et al. (1992) in northeastern Oregon, where birds used an average of 7 roosts (range = 4–11) during a 3–10 month period. These represent minimum values, however, because birds were not tracked every night in either study. Pileated woodpeckers are believed to need multiple roost trees to provide alternative refuges if they are threatened by a predator at a roost site or when roost trees are lost to competitors, windthrow, or decay (Bull et al. 1992). Multiple roost trees also may serve other purposes. Switching roost trees periodically could reduce predation rates. Multiple roost trees may help pileated woodpeckers conserve energy by reducing the distance they fly each day to foraging sites. Because pileated woodpeckers typically drummed after exiting the roost cavity in the morning, multiple roosts may also facilitate territorial defense.

Selection of Sites for Nesting and Roosting

Our results support the hypothesis that selection of nest and roost trees by pileated woodpeckers is influenced by site characteristics. Compared to availability plots, sites around nest and roost trees had higher densities of decadent trees and large snags, and a greater diversity of tree species (Table 5). Pileated woodpeckers probably expend considerable time and energy searching for suitable nest and roost trees. Because decadent trees and snags tend to be patchy in distribution (Bull et al. 1997), pileated woodpeckers may expend less energy finding suitable trees in areas that have higher densities of potential structures to choose from. Site selection also may be influenced by the availability of alternative trees and foraging opportunities. Two or more roost trees in close proximity may be advantageous if a bird is disturbed by a predator while roosting and needs an immediate alternative. During the nesting season, when adults have limited time to search for food, foraging sites close to the nest tree would also provide an energetic advantage. Selection of sites with a high diversity of tree species may reflect not only selection of particular species for nesting and roosting but also increased foraging opportunities, since prey availability and abundance may vary among tree species and decay stages.

Selection for sites with high densities of decadent trees and snags also may reflect a preference for nearby drumming trees. Adult birds call and drum frequently near roost trees as they leave in the morning, and also during excavation of nest cavities in the breeding season. We often observed birds drumming high on the bole of the tallest snags or decadent trees, and we generally could hear the sound of their drumming up to 800 m away. Hard snags or hollow live trees with sound sapwood probably provide optimal drumming sites because fungal decay destroys the elasticity and acoustic quality of wood (Desch and Dinwoodie 1996:100).

Measurements of logs were not useful for distinguishing between used and availability sites. This was not surprising because we rarely saw signs of pileated woodpecker foraging on logs and, when we did, it was generally on logs that were raised off the ground. Pileated woodpeckers also rarely foraged on logs in coastal forests in Oregon (K. Mellen, U.S. Forest Service, personal communication). In contrast, 36% of foraging observations reported by Bull (1987) in northeastern Oregon were on logs. In the wet moisture regimes of coastal forests, logs resting on the ground may become too saturated with water to support colonies of carpenter ants (*Camponotus* spp.), which are the primary food of pileated woodpeckers in this region (Beckwith and Bull 1985; Torgersen and Bull 1995; K. Aubry and C. Raley, unpublished data).

MANAGEMENT IMPLICATIONS

We have proposed elsewhere (Aubry and Raley 2002) that the pileated woodpecker may be a keystone habitat modifier in the Pacific Northwest because it (1) has a unique role in providing nesting or denning sites and foraging opportunities for other species, (2) accelerates decay processes and nutrient cycling, (3) facilitates inoculation by heart-rot fungi, and (4) may mediate insect outbreaks. Accordingly, we have argued that the ecosystem management objectives embodied in the NWFP may be enhanced by giving special attention to the habitat needs of pileated woodpeckers in forest management plans and monitoring activities.

Standards and guidelines in the NWFP for timber harvest on matrix lands in national forests specify that 15% of the harvest area be retained as green trees, including both dispersed trees (30%) and patches 0.2–1.0 ha in size (70%) that include the largest, oldest live trees (both intact and decadent) and hard snags (U.S. Forest Service and U.S. Bureau of Land Management 1994). In addition, NWFP standards and guidelines require that snags be retained (or created) in harvest units at levels adequate to support all species of woodpeckers at 40% of potential population levels as specified in existing management models. The habitat management model developed for pileated woodpeckers in western Washington and Oregon (Neitro et al. 1985:141–145) includes only the number of snags needed for nesting: 6 hard snags ≥63.5 cm dbh for each 40.5 ha harvested; 40% of this level would be 1 large, hard snag for each 17 ha of forest harvested.

Our results indicate that providing adequate nesting and roosting habitat for pileated woodpeckers in coastal forests may require a more comprehensive management strategy. In our study area, pileated woodpeckers used decadent trees as often as snags for both nesting and roosting, and appeared to select for decadent trees. In addition, pileated woodpeckers used an average of 7 roost trees each year, and trees selected for roosting were of different species and had different decay characteristics than those selected for nesting. Because upper-stem heart-rot fungi rarely cause tree death (Bull et al. 1997), living trees infected with such fungi generally will provide suitable nesting and roosting habitat for pileated woodpeckers far longer than a hard snag, which decays relatively rapidly (Cline et al. 1980). Consequently, managing for decadent trees as well as snags would provide both nesting and roosting habitat for pileated woodpeckers, and would provide suitable structures for a much longer period of time than managing only for hard snags.

Although the minimum dbh specified in the model is very similar to the minimum dbh used by pileated woodpeckers for nesting in our study area, several researchers have pointed out the risks associated with managing for woodpecker habitat using minimum values (Conner 1979, McClelland and McClelland 1999). McClelland and McClelland (1999) have argued that the probability of maintaining viable populations of pileated woodpeckers would be enhanced by managing selected tree species for the mean diameter used + 1 SD. In our study area, this would correspond to ranges of 108.6–137.2 cm for western hemlock nest and roost trees, 110.9–128.9 cm for Pacific silver fir nest and roost trees, and 199.6–246.5 cm for western redcedar roost trees.

Sites used by pileated woodpeckers for nesting and roosting had an average of 7.0 large snags and 3.0 decadent trees in each 0.4-ha plot (Table 3). Thus, managing for 1 large, hard snag for each 17 ha of managed forest—an area >40 times larger than our sample plot—is unlikely to provide for the habitat needs of pileated woodpeckers. However, current prescriptions in the NWFP for maintaining the largest, oldest live trees and hard snags in clumped retention areas of harvest units provide managers with opportunities to improve habitat conditions for pileated woodpeckers in managed forests by emphasizing the retention of trees that are most likely to provide nesting or roosting sites. Preserving large live trees and snags that are already infected with upper-stem heart-rot fungi would provide substantial benefits to pileated woodpeckers.

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